DOMESTIC CATS AS PREDATORS AND FACTORS IN WINTER SHORTAGES OF RAPTOR PREY

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The domestic cat (*Felis catus*) was introduced into the United States over 150 years ago. Imported in small numbers for the primary purpose of controlling rodents in our eastern seaboard cities, cats remained scarce for many years. Now an estimated 31 million cats exist across the country (American Humane Association, 1972), and rural cats probably rival in numbers all other large predators combined east of the Great Plains, west of the Sierra Nevada, and in various other localities. In terms of impact on the avifauna, cats may pose little direct threat, for they are reported to kill relatively few birds in most situations (Table 1). Yet as predators on rodents, cats inevitably compete for prey with many of our declining raptors, and therein may lie a serious problem.

Cats are formidable competitors, able to kill rodents at a great and rapid rate. For example, the removal in eight months of over 4200 mice from a 35-acre study plot was ascribed principally to six cats by Pearson (1964). I am not suggesting a cause-and-effect relationship exists between the historical increase of cats and the historical decrease of raptors; however, cats, which are as efficient in their way as guns and DDT, accompany and add another dimension to man's encroachment into wildlife areas. The effects of cat abundance in and about wildlife areas should be monitored as a matter of prudence, especially in view of the decline (see Arbib, 1972) of such formerly "common" raptors as the Red-shouldered Hawk (*Buteo lineatus*), Red-tailed Hawk (*B. jamaicensis*), Marsh Hawk (*Circus cyaneus*), and American Kestrel (*Falco sparverius*), each of which feeds on rodents to a marked degree (May, 1935; MacAtee, 1935).

Most environments in rural America have suffered drastic and repeated alterations; many may be unable today to generate prey in sufficient densities to sustain both raptors and significant numbers of cats. I decided to probe this possibility when a female cat and two of her offspring killed an impressive number of mammals at my home in southern Illinois. I have studied continuously the predation by these cats over the past six years. During this time, shortages in the mammalian prey of hawks have appeared consistently in the cats' hunting grounds each winter. The present report describes and discusses the annual and seasonal predation by these cats from 1 January 1968 through 31 December 1971. Their predation on non-mammalian vertebrates (various birds, reptiles, and frogs) is tabulated to round out the account.

TABLE 1

FREQUENCY OF OCCURRENCE OF VERTEBRATE PREY IN THE DIET OF RURAL CATS[1]

Area	Percent or relative proportion of prey in each group					
	Shrews-moles	Rodents	Rabbits	Birds	Reptiles	Amphibians
Maryland[2]	8	65	12	14	—	—
Pennsylvania[2]	9	60	18	13	—	—
Wisconsin[2]	2	82	5	11	—	—
Michigan[3]	0.9	95.9	0.2	3	—	—
Ontario[3]	Few	Many	—	Few	—	—
Missouri[2]	4	68	12	10	5	1
Oklahoma[2]	Few	Many	Many	Few	Few	Few
Texas[2]	—	65	11	11	13	—
California[2]	—	71	8	20	—	—

[1] Compiled from Bradt, 1949; Eberhard, 1954; Errington, 1936; Hubbs, 1951; Korschgen, 1957; Llewllyn and Uhler, 1952; McMurry and Sperry, 1941; Parmalee, 1953; and Toner, 1956.
[2] Based on analysis of stomach contents.
[3] Based on observed predation.

MATERIALS AND METHODS

The Study Site.—The hunting grounds of the cats centered around our home in fallow farmland near the village of Cobden, Union County, southern Illinois. The area is one of uplands, known as the Shawnee Hills or Illinois Ozarks, which run east to west between the floodplains of the Mississippi and Ohio Rivers. This rolling country was once dominated by forest but now hosts orchards, cultivated crops, old field succession, pastures, second-growth deciduous woods, and impoundments that at many points intercept the natural watersheds.

Characteristically, the area is dotted with small farms, of which my home plot (in 11S, R, 1W, Section 19, Union County) is typical. The house stands atop a knoll, 0.3 mi from the nearest surfaced road and dwelling of a neighbor. An acre of lawn and an aged grove of conifers (*Tsuga*, *Pinus*, *Juniperus*) and deciduous hardwoods (*Quercus*, *Fraxinus*, *Acer*, *Juglans*, *Carya*, *Liquidambar*, *Liriodendron*) surround the house; a barn is close-by. Apple and nectarine (*Pyrus*) orchards (about 50 acres), old fields (25 acres), woods (15 acres), and several impoundments compose the adjacent habitats.

Ground cover in the fields and orchards agree in general composition but differ in height, as a result of differential mowing. In 1968–1971, annual and sometimes biannual mowing occurred on about 75 percent of the total field and orchard acreage. The woods on the plot skirt the fields; one forest-like stretch extends up a ravine to within a few feet of the barn.

The Mammalian Fauna.—The three cats had merely to step out of the barn or off the lawn to enter habitats containing 18 species of possible mammalian prey (Table 2), including three microtines, seven other rodents, three shrews, and the cottontail. Observations, a program of can-trapping for shrews (George, MS), and specimens caught by the cats indicated the summer abundance of these species approximated that reported by Hoffmeister and Mohr (1957) and Layne (1958), shown in Table 2.

TABLE 2

OCCURRENCE AND SUMMER ABUNDANCE OF SMALL TERRESTRIAL MAMMALS (EXCLUDING CARNIVORES) AND THEIR STATUS AS PREY OF WINTERING HAWKS NEAR COBDEN, UNION COUNTY, SOUTHERN ILLINOIS

Species	Summer abundance[1]	Winter status as prey for[2]		
		Red-tailed Hawk	Marsh Hawk	American Kestrel
Opossum (*Didelphis marsupialis*)[3]	C	n	n	n
Eastern mole (*Scalopus aquaticus*)	VC	b	b	b
Long-nosed shrew (*Sorex longirostris*)[4]	U	n	n	n
Short-tailed shrew (*Blarina brevicauda*)	VC	b	b	a
Least shrew (*Cryptotis parva*)[5]	C	n	n	b or n
Woodchuck (*Marmota monax*)[6]	C	n	n	n
Eastern chipmunk (*Tamias striatus*)[6]	C	n	n	n
Eastern gray squirrel (*Sciurus carolinensis*)	U	a or b	b	n
Eastern fox squirrel (*Sciurus niger*)	U	a or b	n	n
Southern flying squirrel (*Glaucomys volans*)[3]	U	n	n	n
White-footed mouse (*Peromyscus leucopus*)[3]	VC	b	b	b
Southern bog lemming (*Synaptomys cooperi*)	U	b	b	b
Prairie vole (*Microtus ochrogaster*)	VC	a	a	a
Pine vole (*Microtus pinetorum*)	C	a	a or b	a or b
Muskrat (*Ondatra zibethicus*)	U	b or n	n	n
House mouse (*Mus musculus*)	C	b	a or b	a
Meadow jumping mouse (*Zapus hudsonius*)[3, 6]	U	n	n	n
Eastern cottontail (*Sylvilagus floridanus*)	VC	a	b	n

[1] VC = very common, C = common, U = uncommon.
[2] a = major, b = minor, n = negligible.
[3] Strongly crepuscular-nocturnal.
[4] Rare in most of southern Illinois.
[5] Taken frequently by owls but seemingly not often by hawks.
[6] Winter hibernator.

Non-feline Predators.—The study plot was ranged over by the following native predators, which, to a greater or lesser extent, competed with the cats for prey the year round (except as noted): various snakes (winter hibernators), Red-tailed Hawk, Marsh Hawk (winter visitant), American Kestrel, Screech Owl (*Otus asio*), Great Horned Owl (*Bubo virginianus*), Barred Owl (*Strix varia*), Long-eared Owl (*Asio otus*; winter visitant), Loggerhead Shrike (*Lanius ludovicianus*), raccoon (*Procyon lotor*), gray fox (*Urocyon cinereoargenteus*), red fox (*Vulpes fulva*), domestic dog (*Canis familiaris*), and perhaps striped skunk (*Mephitis mephitis*). The long-tailed weasel (*Mustela frenata*) and mink (*M. vison*) have been recorded in nearby areas but not on the study site, and evidence is lacking to show that short-tailed shrews, which elsewhere may kill voles, prey on microtines in southern Illinois.

Human predation existed in the form of sportsmen, who annually harvested gray and fox squirrels (1 August to 15 November) and cottontails (11 November to 15 January) within all but the inner core (six acres) of the study plot. A minor amount of trapping was done by me to study the composition of the small mammal fauna, but neither rodent control nor a chemical eradication program was in effect on the study site.

The Cats and Their Habits.—The mother cat, designated Cat 1, was a brindle brought to the study site in 1965. She weighed about eight lbs and was sexually altered in 1967. In 1966 she gave birth to Cat 2 (black female) and Cat 3 (gray male). Both are sexually altered, with Cat 2 weighing 12 lbs and Cat 3 weighing 16 lbs. Prior to the birth of her kittens, Cat 1 caught chiefly house mice, depositing them in the kitchen of my home. She brought rodents and young cottontails to her young, which consumed them with relish. Cats 2 and 3 began to hunt prey, and their mother's prey increased, in 1967. This expansion in predation multiplied our observations and confirmed our impression that detailed information on predation by each member of the group could be obtained. For one thing, the combined home range of the cats only encompassed selected spots within about 17 acres of fields and three acres of woods, with parts of about five adjacent acres of field habitat being used in the late fall and winter months. Secondly, the cats never ate or deposited prey where caught but instead carried it into a "delivery area," consisting of the house and lawn. The exclusive use of this delivery area was verified in 18 to 70 mammal captures per cat, as witnessed between early 1967 and late 1971.

The cats had all assumed definitive patterns of hunting and dietary habits before the study began. Cat 1 sought prey on only about five acres, which she shared with the other two; they in turn shared the balance. Cat 1 ate no prey, hunting fewer hours per day than Cats 2 and 3, each of which consumed about 90–95 percent of the microtine rodents and cottontails that they had captured. They ate varying lower percentages of their other mammalian prey.

Cat 3 was the most successful "mouser." This may have been due to its ability to leap out as much as 6 to 8 feet over 3-foot-high grass, enabling it to reach microtine rodents concealed in runways beneath dense cover. These attacks appeared guided mainly if not entirely by auditory and olfactory cues.

Prior to 1968 and throughout the study a daily allotment per cat of 150–220 g of raw beef, chicken parts, and commercial pet foods was available in the kitchen. An entry in the kitchen door enabled the cats to come and go freely between their hunting grounds and the house. All the cats slept in the house and consumed varying amounts of the food provided for them.

Recording Observed Deliveries of Prey.—Almost all of the outdoor portion of the delivery area and about six acres of the cats' hunting grounds were visible from inside the house; vantage points outside yielded a still wider view of the hunting grounds. Exploiting these advantages, the delivery of prey was monitored from a half hour to 24 hours per day on 1,387 days, during a total of about 8,500 daylight and 7,300 crepuscular-nocturnal hours. Additionally, 17 periods of three to 14 days, involving every season in nearly all the study years, were devoted to continuous monitoring of prey deliveries.

Prey items were usually weighed indoors on a fine balance scale, although a small spring scale, carried outside, was sometimes used. Most sexing was done by external features; the counting of fetuses was done by opening obviously pregnant females before allowing the cats to eat them. The only prey the cats were not allowed to eat were small series of voles appropriated and frozen for future sexing and/or identification.

The delivery area, which was rarely left unattended for longer than 48 consecutive hours, was examined and cleared of prey remains at dawn and dusk when circumstances permitted. This facilitated attribution to diurnal or non-diurnal predation of some whole and many remnant specimens stemming from unobserved deliveries. Specimens not accountable with respect to time of delivery were distributed each month between diurnal, crepuscular, and nocturnal columns, in proportion to the total specimens stemming from observed deliveries of the species. Unobserved deliveries of the day-shunning white-footed and jumping mice were allocated half to crepuscular and half to nocturnal predation, in accordance with the cats' observed pattern of catching these species.

The cats sometimes left the entrails in consuming microtines (bog lemmings, prairie and pine voles) and these remains were difficult to identify as to species. Entrails stemming from unobserved deliveries were allocated to species in ratio to the representation of each microtine in the total monthly captures recorded through observed deliveries.

Besides specimens completely devoured during the absence of observers, gaps in my records and possible misleading information may have resulted from: (a) small prey being swallowed very swiftly and not detected by observers; (b) the scavenging of prey remains by opossums, dogs and other animals, especially at night: and (c) failure to find small prey or remnants concealed under leaves and grass in the delivery area.

RESULTS

Species and Average Annual Totals of Captured Prey.—Mammals taken by the three cats in the four years of study are listed in Table 3, along with the number of fetuses killed, the average weight of the prey specimens, and

TABLE 3

AVERAGE ANNUAL PREDATION (COMBINED) ON VERTEBRATES BY THREE CATS IN UNION COUNTY, SOUTHERN ILLINOIS, 1968–1971

Prey	Number captured[1]	Fetuses killed	Average weight of prey[2]	Combined weight of prey[2]	Percent of catch
Long-nosed shrew	6.0	2.7	3	18	1.3
Eastern chipmunk	19.5	—	60	1150	4.0
White-footed mouse	53.0	32.0	18	954	11.0
Southern bog lemming	26.5	—	25	662	5.5
Prairie vole	202.5	225.7	26	5265	41.9
Pine vole	72.5	26.0	23	1667	15.0
House mouse	19.5	—	12	234	4.0
Meadow jumping mouse	2.5	—	11	27	0.5
Eastern cottontail	46.5	—	165	7672	9.6
Other vertebrates	35.0	—	38	1354	7.2
Totals	483.5	286.4	39	19003	100.0

[1] These figures are double the number of observed captured specimens; see text for explanation.
[2] Figures are to nearest gram.

related data. The figures for total prey are double the logged prey, divided by four. This assumes the study registered 50 percent of the cats' captures—a percentage roughly corresponding to: 1, the average amount of total time the the delivery area was under observation for recording prey; and 2, the number of prey items logged in the same year when the delivery area was under continuous day-and-night scrutiny, compared to the number logged (during equivalent seasonal and hourly periods) when continuously scrutinized for lesser amounts of time. Figures are not available on the rate at which scavengers expunged evidence of unobserved deliveries. If the rate was greater than I believe, the totals for captured prey given in Table 3 are low.

Diurnal predation yielded 49.8 percent of the prey items, crepuscular predation 20.1, and nocturnal predation 30.1 percent. Young cottontails constituted the leading prey by volume (40 percent). Prairie voles were the prey most frequently captured, composing more than 41 percent of all captured vertebrates and 45 percent of the captured mammals. A total of 33.8 percent of the captured prairie voles, plus 18.1 percent of the pine voles, contained fetuses (Table 4), resulting in the average annual removal of over 251 microtine fetuses.

Potential mammalian prey not known to have been caught included all age groups of opossum, mole, short-tailed and least shrews, muskrat, woodchuck, gray, fox and flying squirrels, and native carnivores. In addition, no adults of chipmunks or cottontails were taken, nor fetus-bearing bog lemmings, house mice, and jumping mice.

TABLE 4

SEX RATIOS AND FETUSES IN PREY OF THREE CATS IN UNION COUNTY, SOUTHERN ILLINOIS, 1968–1971

Prey	Percentage of dissected specimens			Average number of fetuses
	Male	Female	Gravid[1]	
Long-nosed shrew (N = 10)	40	60	20	5.5
Eastern chipmunk (N = 36)	44.5	55.5	0	0
White-footed mouse (N = 34)	52.9	47.1	11.1	5.5
Southern bog lemming (N = 23)	52.2	47.8	0	0
Prairie vole (N = 152)	52.6	47.4	33.8	3.3
Pine vole (N = 33)	54.5	45.5	18.1	2.0
House mouse (N = 13)	66.6	33.3	0	0
Meadow jumping mouse (N = 12)	50.0	50.0	0	0

[1] Figures signify percentage of species sample, not percentage of females.

TABLE 5

SEASONAL PERCENTAGE OF PREY CAPTURED IN BROAD DAYLIGHT BY THREE CATS IN UNION COUNTY, SOUTHERN ILLINOIS, IN 1968–1971

Prey	Dec.-Feb.	Mar.-May	June-Aug.	Sept.-Nov.	Total
Long-nosed shrew	0	1.7	1.2	0	2.9
Eastern chipmunk	0	6.8	0.2	2.5	9.5
Southern bog lemming	2.3	2.5	0.2	0.7	5.7
Prairie vole	4.4	18.7	16.2	8.1	47.4
Pine vole	0.5	7.1	1.2	0	8.8
House mouse	0.2	0.2	0.2	0	0.6
Cottontail	0	4.5	6.6	0.2	11.3
Other vertebrates	0	5.1	7.3	1.4	13.8
	7.4	46.6	33.1	12.9	100.0

Comparative Seasonal Success of Diurnal Predation.—Table 5 shows seasonal differences in the frequency with which the cats obtained prey during the non-twilight diurnal hours, which is when most hunting by most hawks occurs. Almost 80 percent of these captures resulted from spring and summer predation, compared to only 7.4 percent for winter predation.

Other Seasonal Patterns of Predation.—In winter the cats sought prey chiefly during the six middle hours of the day, hunting longer on clear bright days than on overcast days, and hunting little at night and on days with both very low temperatures (below 15° F) and dark skies. In spring they hunted without seeming to concentrate on a particular period, although hunting less in mid-day and more often in twilight than before, going abroad infrequently in the middle of the night. In summer and fall they avoided mid-day to hunt mainly in the twilight periods and at night. Freezing weather inconvenienced them, yet they caught prey during and after snow storms and ice glazes; furthermore they rarely missed an opportunity to hunt prey during light rains and immediately after heavy rains.

Records from 24-hour periods of surveillance of the delivery area afford the one consistent means of gauging the average number of combined hours per day the cats devoted to hunting prey. The per day figures were as follows: approximately 14–18 hours in spring; 13–17 hours in summer; 10–15 hours in fall; and 8–12 hours in winter (Cat 1 hunted little in this season).

There were only thirteen 24-hour periods (each in April, May, and June) during which any cat was known to have caught as many as three or more specimens. The greatest number of prey items known to have been caught in a 24-hour period by the combined cats was six, and only three such instances

occurred. The average number of no-capture days per year was 174, of which over 43 percent occurred in the three winter months.

DISCUSSION

The reader who has digested my findings can imagine that a hawk visiting my study site in the winters of 1968–1971 was more apt to see a cat than a rodent. I think this a prudent speculation, and one that I wish to examine in the context of the local concentration of Red-tails, Marsh Hawks, and kestrels in late fall and winter. Although tending to include fewer participants each year (Graber and Golden, 1960; Graber and Graber, 1963), this buildup occurs annually in southern Illinois.

Potentially satisfactory hunting conditions precede the buildup as prey is probably ample and relatively active (and vulnerable) in the mild climate. Annual snowfall averages only about 11 in, as against 22 to 29 in in the central and northern portions of the state (Rodesiler and Qutub, 1973). Absent is the deep and prolonged snow cover that to the north often protects microtine rodents, the prey of greatest importance to these wintering raptors throughout the middlewestern prairie and Great Lakes regions. For example, Craighead and Craighead (1956) found meadow voles (*Microtus pennsylvanicus*) composed 84 to 98 percent of the winter diet of Red-tailed and Marsh Hawks in Michigan, and over 50 percent of that of kestrels. My observations, while limited and scattered over eight years, suggest that in southern Illinois the primary prey are prairie and pine voles, which predominated in the stomach contents of the only wintering, locally killed Red-tailed Hawks (3 specimens), Marsh Hawks (2), and American Kestrels (2) that I have been able to examine.

Birds of these species, under observation from a distance, often obtain what appear to be voles within the general area containing the hunting grounds of my cats. However, I believe that within the cats' home range only few microtines occurred during the winters of my study.

The cats themselves could find little prey of any species from December through February. We logged no specimens on 302 of 361 total winter days. I consider this striking evidence of scarcity of prey, particularly of microtines, which cats detect and seize with special facility. "I have watched cats hunting *Microtus*," Pearson (1960) commented. "The consistent success of their vigils beside runways makes *Microtus*-hunting seem absurdly easy." Other authors bear this out: for example, Bradt (1949) owned a farm cat that killed approximately 1,200 meadow voles of 1,628 mammals caught in 18 months. A cat belonging to Toner (1956) "usually brought in two or three voles each day." Especially my Cat 3, but also Cat 2, almost surely would have caught more microtines in winter if they had been able. They

both relished microtines as food and showed no inclination to omit them from their winter diet. On the contrary, they ate every vole they are known to have captured in winter. As a demonstration of their commitment to winter predation, they increased their home range by about 25 percent. Furthermore, all three cats had the advantage of combing familiar terrain on which they had monitored the microtine populations continuously throughout their hunting years; probably each was well-acquainted with the seasonal activity of these prey, at least by the winter of 1969–70.

As shown in Table 5, the hunting success of my cats rose each spring (peaking in May and June), declined steeply in fall, and became almost nuggatory in the winter months. This cycle almost certainly reflected seasonal differences in density of the prey, especially of microtines. The problem is to know to what extent the cats, by their predation in spring and summer, controlled microtine reproductive cycles the year round, helping cause the depressed winter densities. Annually, from March through November, the cats removed from each acre of their combined home range (25 acres) an average of over 27 mammals-and-fetuses, of which 22.2 per acre were microtines. At the same time, no fewer than 10 species of warm-blooded native predators, along with other kinds of "environmental resistence" (i.e., litters drowned in downpours, specimens killed in mowing operations), presumably reduced the microtine populations still further. With the arrival of late autumn, non-resident hawks may well have been faced by what amounted, by then, to a near-completed harvest of microtines.

Winter Availability of Non-microtine Mammals on the Cats' Hunting Grounds.—A high proportion of the cats' winter hunting was diurnal—thus closely paralleling the diurnal pattern of hawks. It seems possible that hawks seeking mammalian prey in the same place and time as the cats would have enjoyed better hunting had the raptors taken prey that the cats either shunned (moles and shrews), could not catch (squirrels, adult cottontails), or feared to attack (adult native carnivores). Even if this occurred, it is difficult to discover an ample food supply in this list. The squirrels and cottontails consisted of few and wary individuals that had eluded one or more seasons of harvesting by sportsmen and native predators, and that, in the case of the cottontails born on the study site, had escaped the cats, which ate much of the annual crops of young. Few if any vulnerable young carnivores existed on the study site, and normally the woodchucks and chipmunks were in hibernation. The remaining potential prey included mainly moles, shrews, the few white-footed mice active on dark days and in twilight periods, and house mice; the last tended to overwinter in and around buildings, where they were more available to the cats than to hawks. As moles spend little time foraging above ground at any time, especially in winter (Hoffmeister

and Mohr, 1957), the supply of sizeable prey for hawks would appear to have been contracted seriously in the absence or unavailability of microtine rodents. I doubt that shrews, weighing only 2.7 g to 11.6 g on the study site, could have represented more than an augmentation in the diet of Redtails, although perhaps important to Marsh Hawks and kestrels in the absence of other prey.

The Prairie Vole As Primary Prey of Hawks and Cats.—Prairie voles, I believe, would thus typically be the basic mammalian food for wintering buteos, harriers and kestrels throughout most of southern Illinois. This species frequents grassy habitats of many types (Hoffmeister and Mohr, op. cit.), haunts surface runways in daylight (except perhaps in the coldest weather), and has a tendency to develop strong populations due to a high reproductive rate (Krebs et al, 1969). Bog lemmings and pine voles are more specialized and more limited in distribution, as well as "sporadic in occurrence and usually uncommon" (Hoffmeister and Mohr, op. cit.). Accordingly, the impact of annual cat predation on the availability of prairie voles could well pose the principal threat to the success of wintering hawks in my area of study. Fetus-bearing specimens (Table 4) constituted over one-third of the prairie voles taken by my cats, and this figure excludes fertilized females in which pregnancy was undetected by the methods that I employed.

After investigating the intensity and bioenergetics of carnivore (mainly cat) predation on the California vole (*Microtus californicus*), Pearson (1964, 1966, 1971) argued that population cycles of microtine rodents may be controlled by carnivores. "The data support the theory that carnivore predation during a crash and especially during the early stages of the subsequent population low determines to a large extent the amplitude and timing of the microtine cycle of abundance." In other words, if a powerful force of carnivores remains active in the habitats of a depleted and vulnerable species of preferred prey, the carnivores may check and overpower the breeding of the prey. Cats that are fed by man, as were mine, will inevitably remain a significant force on their hunting grounds the year round, in contrast to native predators, which tend to increase and decrease in an area according to the availability of prey. If prey animals grow scarce or difficult to catch, cats with a guaranteed food supply are merely inconvenienced, whereas native predators either must leave for "greener pastures" (i.e., hawks) or face unpromising prospects and even starvation (Thompson, 1935; Pearson, 1966; Pitelka, 1961).

Krebs et al. (1969) conducted a two-year study of the cyclic demography of the prairie vole in southern Indiana. They determined maximum density to be 35–40 specimens (not including fetuses and nest litters) per acre, under more-or-less natural conditions in a favorable habitat, but usually density was

much lower, ranging from about two to 15 individuals (of "trappable" size) per acre. The Indiana study also found the prairie vole to be relatively trappable and thus easily trapped out. Given such vulnerability, spring and summer reproduction of prairie voles might be curtailed and its amplitude reduced by cats, as by trapping. This would reduce local population levels severely enough that reproduction in the non-winter months would not provide a winter abundance of specimens.

Work now in progress at my study site is investigating these and related problems, which are fraught with the complexities of environmental relationships that regulate the density of species in a given habitat at a given time (see Holling, 1959, 1965). Meanwhile, I think it is worth emphasizing that the distribution and number of cats in rural habitats are regulated less by the carrying capacity of the land and environmental resistence than by the customs and needs of the human population. No one knows how many cats are hunting prey in any part of the American country side. I recently received information from 45 of 49 queried wildlife protective agencies on the continental distribution and density of cats in the U. S.; most expressed a desire to be helpful but none furnished data established by a cat census.

PROJECTIONS

On the assumption that one-third of the estimated 31 million U. S. cats occurs in rural areas, our countryside contains 10,333,333 cats. Assuming each such cat catches prey at the same average annual rate and exploits the same average number of acres per animal as the average of my cats, then cats are removing about 5.5 billion rodents and fetuses and about 2.5 billion other vertebrates per year from a total of about 26,000 mi.^{2} These are conservative projections, for they do not take into account young rodents that starve to death as a result of predation on lactating mothers, or the magnitude of predation by cats that catch most of their own food and more completely live "off the land." In terms of whole prey, the food requirement of one cat is about 180 g per day, or 65,700 g per year (Howard, 1957; Bouliere, 1962). My cats together did not satisfy this level during any year, nor did they in any extended period even in the spring and summer months. Yet many "farm" cats meet most of their annual food requirements by predation, with food subsidies being given them chiefly during periods when their loss of weight and begging behavior point to prey shortages (personal observation).

SUMMARY

A continuous study of predation by three rural cats was conducted in Union County, southern Illinois, from 1 January 1968 through 31 December 1971. The results estab-

lished a basis for examining the possibility that cat predation may result in depleted winter populations of microtine rodents and other prey of Red-tailed Hawks, Marsh Hawks, and American Kestrels.

Although one of the three cats never ate prey and each cat was assured an ample supply of daily food at home, all captured prey. Their combined predation removed an annual average of 483.5 vertebrates and 286.4 mammalian fetuses from a combined home range of 22 acres of field habitat and three acres of woods. By volume, the principal prey were non-adult cottontails, by frequency of captures, prairie voles. Rodents of seven species constituted 81.9 percent of the total combined diurnal-crepuscular-nocturnal catch, and over 95 percent of the crepuscular-nocturnal catch.

The cats obtained 92.6 percent of their average annual diurnal captures between 1 March and 30 November. Their hunting success in winter was very poor, probably as a result of prey shortages that their own prior predation may have helped create. It is suggested that when captures of preferred prey by skillful, experienced cats on their natal hunting grounds sharply decline, the home range of the cats contains few such prey for rodent-seeking hawks.

ACKNOWLEDGMENTS

My wife, Marian, fed the cats and assisted in every imaginable way to record their activities. I wish particularly to thank her, as well as express my gratitude to Shelly Bleiweis and Howard Stains, who dissected some of the specimens of prey, and Clark Casler, Tad Cooper, David Crotty, Marian Fabbri, James Fuller, and Ann Thomas, who helped log the captures of prey.

LITERATURE CITED

American Humane Association. 1972. Animal control survey. Amer. Humane Assoc., Denver.

Arbib, R. 1972. The blue list of 1973. Amer. Birds, 26:932–933.

Bouliere, F. B. 1962. The natural history of mammals. A Knopf, New York.

Bradt, G. W. 1949. Farm cat as a predator. Michigan Conservation, 18:23–25.

Craighead, J. J. and F. C. Craighead, Jr. 1956. Hawks, owls and wildlife. Stackpole, Harrisburg, Pa.

Eberhard, T. 1954. Food habits of Pennsylvania house cats. J. Wildlife Mgmt., 18: 284–286.

Errington, P. L. Notes on food habits of southern Wisconsin house cats. J. Mammal., 17:64–65.

Graber, R. and J. S. Golden. 1960. Hawks and owls: population trends from Illinois Christmas counts. Ill. Nat. Hist. Survey, Biol. Notes, No. 41.

Graber, R. R. and J. W. Graber. 1963. A comparative study of bird populations in Illinois, 1906–1909 and 1956–1958. Ill. Nat. Hist. Survey, Bull., 28:378–582.

Hoffmeister, D. F. and W. M. Mohr. 1957. Fieldbook of Illinois mammals. Ill. Nat. Hist. Survey Div., Manual 4.

Holling, C. S. 1959. The components of predation as revealed by a study of small mammal predation of the European pine sawfly. Canadian Ent., 91:293–320.

Holling, C. S. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. Ent. Soc. of Canada, Mem. No. 45.

Howard, W. E. 1957. Amount of food eaten by small carnivores. J. Mammal., 38: 516–517.

Hubbs, E. L. 1951. Food habits of feral house cats in the Sacramento Valley. Calif. Fish and Game, 37:177–189.

Korschgen, L. L. 1957. Food habits of coyotes, foxes, house cats and bobcats. Missouri Conser. Comm., Bull. No. 15.

Krebs, C. J., B. L. Keller, and R. H. Tamarin. 1969. *Microtus* population biology: demographic changes in fluctuating populations of *M. ochrogaster* and *M. pennsylvanicus* in southern Indiana. Ecol., 50:587–607.

Layne, J. N. 1958. Notes on mammals of southern Illinois. Amer. Midl. Nat., 60: 219–254.

Llewellyn, L. M. and F. M. Uhler. 1952. The foods of fur animals of the Paxtuxent Research Refuge, Maryland. Amer. Midl. Nat., 48:193–203.

MacAtee, W. L. 1935. Food habits of common hawks. U. S. Dept. Agric., Circ. 370.

May, J. B. 1935. The hawks of North America. Nat. Assoc. Audubon Soc., New York.

McMurry, F. B. and C. C. Sperry. 1941. Food of feral house cats in Oklahoma, a program report. J. Mammal., 22:185–190.

Parmalee, P. W. 1953. Food habits of the feral house cat in east-central Texas. J. Wildlife Mgmt., 19:375–376.

Pearson, O. P. Carnivore-mouse predation: an example of its intensity and bioenergetics. J. Mammal., 45:177–188.

Pearson, O. P. 1966. The prey of carnivores during one cycle of mouse abundance. J. Anim. Ecol., 35:217–233.

Pearson, O. P. 1971. Additional measurements of the impact of carnivores on California voles (*Microtus californicus*). J. Mammal., 52:41–49.

Pitelka, F. A. 1961. Ecology of lemmings and other microtines in northern Alaska. Arctic Inst. of North America, Report 1960–1961.

Rodesiler, J. and M. Qutub. 1973. Precipitation in Illinois. Trans. Ill. Acad. Sci., 66:61–76.

Thompson, D. Q. 1955. Ecology of the lemmings. Arctic Inst. of North America, Final report.

Toner, G. C. 1956. House cat predation on small mammals. J. Mammal., 37:119.

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